Selecting Biological Reserves Cost-Effectively: An Application to Terrestrial Vertebrate Conservation in Oregon

Stephen Polasky, Jeffrey D. Camm, and Brian Garber-Yonts

ABSTRACT. Concerns that the loss of habitat have greatly increased species extinction rates has led to calls for establishing biological reserves to preserve key habitat. In this paper, we study reserve site selection for terrestrial vertebrates in Oregon using data on species ranges and land values. We find cost-effective strategies that represent a maximum number of species for a given conservation budget. By varying the budget, we find the cost of obtaining various levels of representation. In general, effective conservation decision-making requires integrated analysis of both biological and economic data. (JEL Q20)

I. INTRODUCTION

In many parts of the world, population growth and economic expansion have increased the percentage of land devoted to human use. There has been widespread conversion of habitat for agriculture and timber harvesting, and to a lesser extent urban development. There are concerns that the loss of habitat has greatly increased species extinction rates (Wilson 1988; Pimm et al. 1995). Such concerns have lead to calls for public policies and private actions to protect species and their habitats. In the United States, the Endangered Species Act prohibits actions that harm species listed under the Act as endangered or threatened and seeks to promote the recovery of all such species. Internationally, the Convention on Biological Diversity, drafted for the 1992 U.N. Conference on Environment and Development, seeks to promote the conservation of biodiversity among signatory countries. In addition, many private non-profit organizations are actively involved in the conservation of species and

A commonly used strategy to conserve biological diversity is the establishment of biological reserves to preserve key habitat. Examples of this approach include the National Wildlife Refuge system and biological reserves established by private groups such as the Nature Conservancy. As is readily recognized by most conservationists, the resources available for conservation are not sufficient to protect all habitats and species. Therefore, it is necessary to choose conservation priorities. The question of where to locate biological reserves is a classic economic problem involving the allocation of a limited budget to maximize a desired goal (in this case, the conservation of biological diversity). Despite the relevance of an economic approach, to date economists have not been centrally involved in the analysis of issues such as location of biological reserves, or more generally, in analyzing and informing conservation

There is an extensive literature in conservation biology on choosing the best locations for biological reserves (e.g., Kirkpatrick 1983; Margules, Nicholls, and Pressey 1988; Pressey et al. 1993; Vane-Wright, Humphries, and Williams 1991; Williams et al. 1996). Typically, biological reserve sites are

Stephen Polasky is Fesler-Lampert Professor of Ecological/Environmental Economics Department of Applied Economics, at the University of Minnesota. Jeffrey Camm is professor and head of the Department of Quantitative Analysis and Operations Management, College of Business Administration at the University of Cincinnati. Brian Garber-Yonts is an economist with the U.S.D.A. Forest Service in Corvallis, Oregon.

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selected to cover the maximum number species given a constraint on the total number of sites that can be included (Church, Stoms, and Davis 1996; Cocks and Baird 1989; Csuti et al. 1997; Kiester et al. 1996; Saetersdal et al 1993; Willis et al. 1996). A species is covered when it occurs in at least one selected reserve site. We refer to this approach as site-constrained reserve site selection. Implicit in this approach is the assumption that there is equal cost to establishing a reserve at each potential reserve site. In reality, however, there are often large cost differences across sites.

In a recent study using data on the locations of endangered species and average land value by county for the United States, Ando et al. (1998) solved a budget-constrained, reserve site selection problem. Under a budgetconstrained approach, a set of selected sites is a feasible reserve system, regardless of the number of selected sites, if and only if, the sum of the costs of the selected sites is less than or equal to the conservation budget. Ando et al. (1998) compared the costs of covering the same number of species under both the budget-constrained and site-constrained approaches. They found that the costs of achieving a given level of species coverage were far lower with the budgetconstrained approach. For example, the cost to cover approximately one-half of the 911 endangered species in the database under the budget-constrained approach was less than one-third the cost of the site-constrained ap-

In this paper, we study reserve site selection incorporating differences in land cost using data on the distribution of terrestrial vertebrates and land values in Oregon. Focusing on a single state, rather than the entire country, allows us to gather more detailed data and analyze patterns at a finer geographic scale. The Oregon data, while not perfect, offers several advantages over the county level data used in Ando et al. (1998). Counties can be quite large and diverse. For example, the area of San Bernadino County in California is 51,961 km². Large counties may cover a range of different habitat types, each with different sets of species, and have widely different land values across different parts of the county. In this study, the maximum size of any potential reserve site is 635 km², which reduces the problem of habitat and land value variability within a site. Further, land value data in this paper are based on assessed market value of all non-urban land, rather than just agricultural land, which better represents the value of land that may be set-aside for conservation. Finally, we use data on the geographic ranges for all species in a taxonomic group, terrestrial vertebrates, rather than just endangered species. Some conservation biologists have argued that it is important to save habitat for all species, not just those currently on the endangered species list, because without protection other species will become endangered in the future. However, since the data are limited to terrestrial vertebrates, the results in this paper should not be interpreted as necessarily finding the best sites to conserve other taxonomic groups or for conserving all biodiversity in

In the next section, we describe the data used in this study. Section 3 presents the reserve site selection problem and methods for finding an optimal solution to this problem. Section 4 presents results of the reserve site selection problem using the Oregon data. We compare the results of the budget-constrained approach with those of the site-constrained approach. The final section contains a discussion of important additional issues.

II. DATA

Analyzing the optimal location of biological reserves under a budget constraint requires integrating economic and biological data. In this paper we used: a) biogeographic data that describes the range of each species; and b) land value data that describes the opportunity cost of designating any given site as a biological reserve. The study area, roughly the western two-thirds of the State of Oregon, was partitioned into 289 sites by overlaying a hexagonal grid used in the EPA Emap program. Each hexagonal grid has an area equal to 635 km².

The biogeographic data were originally compiled from records of the Nature Conservancy's Natural Heritage Program, and other

sources, for the Biodiversity Research Consortium—a cooperative agreement among various government agencies for the purposes of collecting and analyzing patterns of biodiversity. A detailed description of this data set is given in Master et al. (1995). The data set includes information on species ranges for all 415 terrestrial vertebrates that breed in the study area. The study was limited to terrestrial vertebrates because the geographic distributions of these species are among the best known. The 415 species consist of 248 bird species, 113 mammalian species, 28 reptilian species and 26 amphibian species. At each of the 289 sites, each species was placed into one of four categories: a) confident—a verified sighting of the species at the site had occurred in the past two decades; b) probable—the site contains suitable habitat for the species and there have been verified sightings nearby; c) possible—no verified sightings have occurred at the site and the site is of questionable suitability for the species; d) not present—habitat is unsuitable for the species. For the purposes of this study, a species was assumed to occur at a site if and only if it was in the confident or probable categories at the site. Polasky et al. (2000) assign probabilities for the "probable" and "possible" categories and maximize expected coverage in a site-constrained problem. Figure 1 illustrates the pattern in the number of species that occur at each site. The Klamath Lake area near the California border has the greatest collection of species of any region in the study area. There is not great variation in the number of species that occur at each site, however, with a minimum of 164 species and a maximum of 265 species.

In this study, the opportunity cost of designating a site as a biological reserve is assumed to be the average per acre land value at the site. In a perfectly functioning competitive market, the price of land equals the net present value that accrues from land ownership. If this value is foregone when the site is designated as a biological reserve, then land costs are the appropriate measure of opportunity cost. Some values such as the value of recreation may not be lost when the site is designated as a biological reserve. In addi-

tion, there may be important public goods or externalities so that the full social value of the land is not captured by market price. For example, a parcel of undeveloped land may provide ecosystem services, such as water purification, or visual amenities to non-owners. Data sufficient to capture such benefits does not exist. Further, real land markets often fall short of the competitive ideal so that the market price may not be an accurate signal of value. Also, data on assessed market value, which is used in this study, does not always accurately reflect market value. Therefore, the land value data used in this study should be viewed as a proxy for, not a complete measure of, the opportunity cost of designating a site as a biological reserve.

Details of the methods used to find the average land value figures for the 289 sites in this study are described in Garber-Yonts and Polasky (1998). For private land, computerized records of assessed market values were available for a majority of counties in Oregon. However, such records were not available for a number of counties in eastern Oregon, which limited our study area to roughly the western two-thirds of the state. For public land, no equivalent measure of market value exists. Instead, for the value of public land we estimated the potential net present value of resources generated on public land, using forest inventory and productivity data and livestock forage productivity. Public lands where commodity production is not allowed, such as wilderness areas and national parks, were assumed to have no opportunity costs. Urban land, defined as land within urban growth boundaries, which are required by Oregon land use laws for every city and town in Oregon, and tribally owned land were excluded from the analysis.

Figure 2 shows land values by site. Land values tend to be higher west of the Cascade Range. Land values are highest in the Willamette Valley in the northwest part of the State, particularly on the outskirts of the Portland metropolitan area, in the Rogue River Valley in the southwest part of the state, near the city of Bend in central Oregon, and along the coast. The lowest land values occur in the dry southeastern part of the study area, for which the only significant

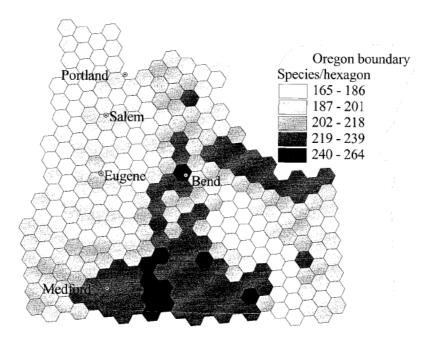


FIGURE 1 Species Richness by Hexagon

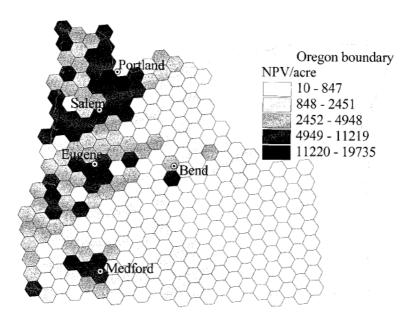


FIGURE 2
PER ACRE LAND VALUE BY HEXAGON

component of value is livestock forage production.

III. THE SITE-CONSTRAINED AND BUDGET-CONSTRAINED RESERVE SITE SELECTION PROBLEMS

Much of the previous work in reserve site selection has solved the problem of maximizing the species included in a reserve network, subject to a restriction on network size. (See for example, Arthur et al. 1997; Camm et al. 1996; Church et al. 1996; and Csuti et al. 1997.) In the operations research literature, this problem is known as the maximal covering location problem (MCLP). Church and ReVelle (1974) first formulated MCLP as an integer-programming problem. The integer programming formulation for the reserve site selection problem is as follows:

Let

 $x_j = 1$ if site j is chosen, 0 if not, $j = 1, \ldots, n$

 $y_i = 1$ if species *i* is covered, 0 if not, $i = 1, 2, \dots, m$

 N_i = the set of candidate sites that contain species i

k = maximum number of sites to be chosen

MCLP:

$$\max \sum_{i=1}^{m} y_i,$$
 [1]

subject to:

$$\sum_{i \in \mathcal{N}} x_j \ge y_i, i = 1, 2, \dots, m$$
 [2]

$$\sum_{i=1}^{n} x_{i} \le k.$$
 [3]

The objective function [1] is to maximize the number of species included in the network. Constraint set [2] ensures that species i is not counted as included if no site in which it occurs is selected. Constraint [3] limits the number of sites in the reserve network to k.

In this work, as in that of Ando et al. (1998), we are concerned with an extension

of MCLP, the budget-constrained maximal covering location problem (BCMCLP): BCMCLP:

$$\max \sum_{i=1}^{m} y_{i},$$
 [4]

subject to:

$$\sum_{i \in N_i} x_j \ge y_i, i = 1, 2, \dots, m$$
 [5]

$$\sum_{i=1}^{n} b_{i} x_{j} \le B, \tag{6}$$

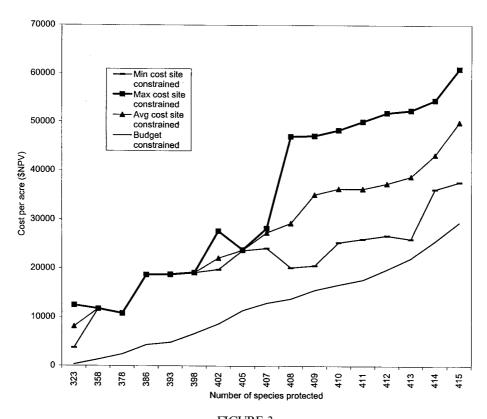
where $b_j > 0$ is the opportunity cost of choosing a reserve at location j and B > 0 is the budget available for locating reserves.

For the Oregon data, which contains 289 sites and 415 species, BCMCLP has 704 variables (289 x_j variables and 415 y_i variables) and 416 constraints (415 constraints of type [5] and one of [6]). This problem is solved using the optimization software Cplex 6.0 (CPLEX 1995).

IV. RESULTS

In this section, we present the results of solving both the site-constrained and the budget-constrained, reserve site selection problems described in the prior section using the Oregon terrestrial vertebrate and land value data described in Section 2. We solved these problems for a range of constraints on the number of sites and the size of the budget.

We summarize the results of the solutions of the site-constrained, and budget-constrained reserve site selection problems in Figure 3. The coverage of species is measured along the horizontal axis. The cost to attain a given level of coverage is measured along the vertical axis. The solution to the site-constrained problem is often not unique. For k = 2, and k > 5, there are multiple combinations of sites that generate an optimal solution. For k < 10, there are no more than four combinations of sites that generate an optimal solution, often with very similar costs. For k > 10, however, there are more



 $\label{eq:FIGURE 3} \textbf{Species Coverage Cost Curve (Budget-Constrained and Site-Constrained)}$

than 200 combinations that generate an optimal solution, often with quite different costs. We plot the minimum, average, and maximum cost for up to 200 randomly chosen solutions in the case where there are multiple solutions.

As shown in Figure 3, a given level of coverage is typically far less costly under the budget-constrained approach than under the site-constrained approach. For coverage up to 350 species, the cost of the budget-constrained solution is less than 10% of the cost of the site-constrained solution. Using a site-constrained approach, which ignores differences in cost between sites, can yield grossly inefficient solutions. The inefficiency of the site-constrained approach is likely to be large in cases like in Oregon where there is greater variation in land costs across sites than in species richness. Conservation planners who ignore economic considerations in assessing

conservation priorities risk wasting large portions of their scarce conservation budgets.

The difference in cost between the site-constrained and the budget-constrained solutions diminishes in percentage terms as coverage rises to complete coverage. Several species in the data set have extremely restricted ranges, including five species whose range is limited to a single site. Covering these species requires the inclusion of certain sites under either approach, which makes the cost of the two approaches more similar, at least in percentage terms.

Several other important points also come out clearly in Figure 3. Under the budget-constrained approach, the cost of covering the majority of species is quite modest compared to the cost of covering the final few species. Over 75% of the species can be covered at approximately 1% of the total cost of covering all species. Covering the final 10

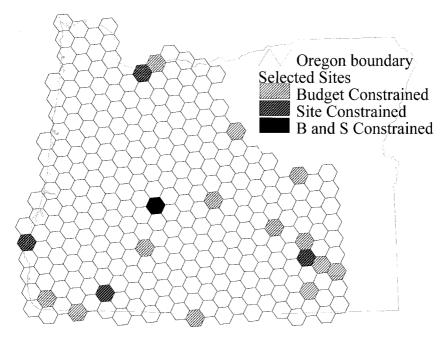


FIGURE 4
BUDGET-CONSTRAINED AND SITE-CONSTRAINED SOLUTIONS
FOR SPECIES COVERAGE OF 385 SPECIES

species costs more than covering the first 405 species. Covering the last species, that is, increasing coverage from 414 to 415 species, costs more than covering the first 378 species. It is interesting to note that the last species covered is the lynx (*Lynx Canadensis*), which is currently under consideration for inclusion on the endangered species list. The lynx occurs in only two sites in our data, both of which are relatively expensive. Many species, however, are wide-ranging and are contained in numerous sites. There are 132 species that occur in 200 or more sites, including 64 species that occur in all 289 sites. Conversely, this means that many sites contain a large number of species. The first sites selected are those that have both a large number of species and low land values. In contrast, covering each of the last species requires including an additional site for each additional species with the most costly additional site added at the last step.

Figures 4 and 5 show the location of sites chosen under both the site-constrained and

budget-constrained approaches for two different levels of coverage. Under the site-constrained approach, it takes a minimum of five sites to cover 385 species. Far more sites are selected under the budget-constrained approach, but as noted above, the collection of these sites is far less expensive. In the eastern part of the study area where land is inexpensive, nine sites are chosen under the budgetconstrained approach while only one site is chosen under the site-constrained approach. In the western and central part of the study area where land costs are higher, both approaches select reserve sites in the same general regions to represent different collections of species. Within these general areas, however, the site-constrained approach generally chooses species rich sites while the budgetconstrained approach chooses lower cost sites. Figure 5 shows the solution of the two approaches for complete coverage of 415 species. The pattern of site selection under the two approaches does not show the obvious split between regions shown in Figure 4.

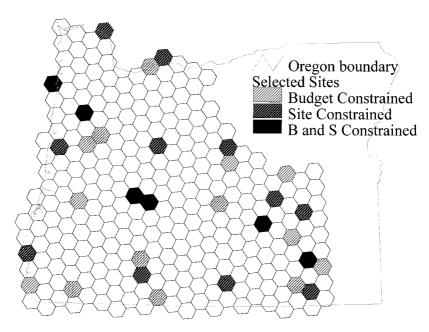


FIGURE 5
BUDGET-CONSTRAINED AND SITE-CONSTRAINED SOLUTIONS
FOR SPECIES COVERAGE OF 415 SPECIES

Flexibility in choosing sites is limited by the constraint that all species much be covered, including the five species that are present in a single site and the 36 species that are present in 10 or fewer sites.

V. DISCUSSION

In this paper, we showed that casting the problem of locating biological reserves as a budget-constrained problem that incorporates differential land cost, rather than as a siteconstrained problem ignoring land cost differences, results in far more cost-effective conservation. The percentage cost savings under the budget-constrained approach visà-vis the site-constrained approach is even larger than in Ando et al. (1998). Ando et al. (1998) uses endangered species whose ranges are often quite limited, which reduces the flexibility in site selection. On the other hand, the Oregon data on terrestrial vertebrates have many wide-ranging species, which allows for greater flexibility to choose sites with low cost, resulting in greater savings from adopting a budget-constrained approach.

While this paper has demonstrated the relevance of taking into account land cost differences in conservation decisions, there is a more general lesson to be drawn from this work: economic analysis is useful in analyzing strategies to conserve biological diversity. The resources devoted to conservation fall far short of the resources necessary to conserve all biodiversity. The problem of allocating scarce resources to achieve desired ends is a textbook definition of an economic problem. Economic analysis can illuminate cost-effective solutions to conservation problems and has wider applicability to conservation decision-making than has been utilized to date.

The objective function we used in this paper was quite simple, namely to maximize the number of species represented in a reserve network. Under this objective, all species have the same conservation value. It is reasonable to think that some species may be more valuable to conserve than others (e.g.,

game species or charismatic megafauna). If so, a weight could be attached to each species indicating its relative worth. Formally, the objective function could then be written as:

$$\max \sum_{i=1}^{m} a_i y_i,$$
 [7]

where a_i is the weight for species i. Solving a site-constrained or budget-constrained problem with unequal weights is technically no more difficult than solving with equal weights. However, establishing what the appropriate weights actually are is a large research question.

Another approach is to conserve a measure of diversity rather than just a weighted or un-weighted function of species numbers (e.g., Faith 1992; May 1990; Solow, Polasky, and Broadus 1993; Vane-Wright, Humphries, and Williams 1991, Weitzman 1992). Under a diversity measure approach, the value of a given species is not a constant but depends upon what other species are also conserved. A species that has lost all close remaining genetic relatives may have great conservation value, but would have less value if a close genetic relative were also conserved. In practice, choosing sites based on a measure of diversity versus the number of species generally yields similar results (Haecker, Cowlishaw, and Williams 1998; Polasky et al. 2001; Williams and Humphries 1996) because diversity measures and the number of species tend to be highly positively correlated.

All of the objectives considered above are based on presence of the species in at least one location versus being totally absent. An objective based on global presence/absence can be justified on the basis that conserving the species someplace is necessary to preserve the genetic information or evolutionary potential of the species. However, there are additional benefits to conservation besides these. The population size of a species or the location of the species may be important as well. For example, having a large population of a species close to human population centers may increase the benefits from wildlife-

based recreation. Including a location specific value for conserving a species can be handled in site-constrained or budget-constrained problems by modifying the objective function as follows:

$$\max \sum_{i=1}^{m} \sum_{i=1}^{n} a_{ij} x_{ij} y_{i},$$
 [8]

where a_{ij} is the weight attached to conserving species i at site j. The value of conserving a species at a given site may depend on whether the species is conserved at other sites, in which case a_{ij} will be a function of some or all x_j variables. Incorporating population size, rather than just presence or absence at a given site, requires more detailed biological information on habitat preference of species, habitat availability and quality.

The results of this paper, while suggestive of good locations for biological reserves in Oregon, are only a first step in the analysis. More refined biological and economic data are needed before the results of such analysis could be used to give advice to decisionmakers. An important step that needs to be taken in this line of research is to connect land management actions to both biological and economic consequences. In this analysis, we made two important simplifications. First, a site was either a reserve, or it was not. Second, species were treated as conserved, if and only if, they were contained in at least one reserve site. In reality, there are multiple management options and multiple gradations in the quality of habitat for species. The probability of survival for a species depends upon the quantity, quality, and spatial pattern of habitat. Several recent studies have integrated population biology modeling and economic analysis to assess the tradeoff between species survival and economic returns for a single species (Haight 1995; Montgomery, Brown, and Adams 1994; Marshall, Haight, and Homans 1998). Montgomery et al. (1999) illustrate the cost of conserving species under alternative land use plans for Monroe Country, Pennsylvania. Integrating population biology models with the economic consequences of alternative management for groups of species over a wide geographic area remains a challenge. Future work should attempt to incorporate the biological and economic consequences of alternative land management to capture more of the important, but complex, reality inherent in conservation decision-making.

References

- Ando, Amy, Jeffrey Camm, Stephen Polasky, and Andrew Solow. 1998. "Species Distributions, Land Values, and Efficient Conservation." Science 279 (27 Mar.): 2126–28.
- Arthur, Jeffrey L., Mark Hachey, Kevin Sahr,
 Manuela Huso, and A. Ross Keister. 1997.
 "Finding All Optimal Solutions to the Reserve Site Selection Problem: Formulation and Computational Analysis." Environmental and Ecological Statistics 4:153–65.
- Camm, Jeffrey, Stephen Polasky, Andrew Solow, and Blair Csuti. 1996. "A Note on Optimal Algorithms for Reserve Site Selection." Biological Conservation 78 (3): 353–58.
- Church, Richard, and Charles ReVelle. 1974. "The Maximal Covering Location Problem." Papers of the Regional Science Association 32:101–18.
- Church, Richard, David Stoms, and Frank Davis. 1996. "Reserve Selection as a Maximal Coverage Location Problem." *Biological Conservation* 76 (2): 105–12.
- CPLEX Optimization Inc. 1995. *Using the Cplex Callable Library*. Inuline Village, Nev.: ILOG-CPLEX Division.
- Cocks, K. D., and I. A. Baird. 1989. "Using Mathematical Programming to Address the Multiple Reserve Selection Problem: An Example from the Eyre Peninsula, South Australia." *Biological Conservation* 49 (2): 113–30.
- Csuti, Blair, Stephen Polasky, Paul Williams, Robert Pressey, Jeffrey Camm, Melanie Kershaw, Ross Kiester, Brian Downs, Richard Hamilton, Manuela Huso, and Kevin Sahr. 1997. "A Comparison of Reserve Selection Algorithms Using Data on Terrestrial Vertebrates in Oregon." *Biological Conservation* 80 (1): 83–97.
- Faith, Daniel P. 1992. "Conservation Evaluation and Phylogenetic Diversity." *Biological Conservation* 61 (1): 1–10.
- Garber-Yonts, Brian, and Stephen Polasky. 1998. Oregon Land Values Dataset Manual. Oregon

- Multiscale Biodiversity Conservation Project, Oregon Fish and Wildlife Department.
- Haecker, Jocelyn E., Guy Cowlishaw, and Paul H. Williams. 1998. "Patterns of African Primate Diversity and Their Evaluation for the Selection of Conservation Areas." *Biological Conservation* 84 (3): 251–62.
- Haight, Robert. 1995. "Comparing Extinction Risk and Economic Cost in Wildlife Conservation Planning." *Ecological Applications* 5 (3): 767–75.
- Kiester, A. Ross, J. Michael Scott, Blair Csuti, Reed Noss, Bart Butterfield, Kevin Sahr, and Denis White. 1996. "Conservation Priorities Using GAP Data." Conservation Biology 10 (5): 1332–42.
- Kirkpatrick, J. B. 1983. "An Iterative Method for Establishing Priorities for the Selection of Nature Reserves: An Example from Tasmania." *Biological Conservation* 25 (2): 127–34.
- Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. "Selecting Networks of Reserves to Maximize Biological Diversity." *Biological Conservation* 43 (1): 63–76.
- Marshall, Elizabeth, Robert Haight, and Frances Homans. 1998. "Incorporating Environmental Uncertainty into Species Decisions: Kirkland's Warbler Habitat as a Case Study." *Conservation Biology* 12 (5): 975–85.
- Master, Larry, Nancy Clupper, Eleanor Gaines, Chris Bogert, Rob Solomon, and Margaret Ormes. 1995. *Biodiversity Research Consortium Species Database Manual*. Boston: The Nature Conservancy.
- May, Robert M. 1990. "Taxonomy as Destiny." *Nature* 347 (13 September): 129–30.
- Montgomery, Claire, Gardner Brown, Jr., and Darius Adams. 1994. "The Marginal Cost of Species Preservation: The Northern Spotted Owl." Journal of Environmental Economics and Management 26 (2): 111–82.
- Montgomery, Claire, Robert Pollak, Kathryn Freemark, and Denis White. 1999. "Pricing Biodiversity." Journal of Environmental Economics and Management 38 (1): 1–19.
- Pimm, Stuart L., Gareth J. Russell, John L. Gittleman, and Thomas M. Brooks. 1995. "The Future of Biodiversity." *Science* 269 (21 July): 347–50.
- Polasky, Stephen, Jeffrey D. Camm, Andrew R. Solow, Blair Csuti, Denis White and Rugang Ding. 2000. "Choosing Reserve Networks with Incomplete Species Information." *Biological Conservation* 94 (1): 1–10.
- Polasky, Stephen, Blair Csuti, Christian Vossler, and S. Mark Meyers. 2001. "Using Taxo-

- nomic Distinctness to Prioritize Sites for North American Birds.' *Biological Conservation* 97 (1): 99–105.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. "Beyond Opportunism: Key Principles for Systematic Reserve Selection." *Trends in Ecology and Evolution* 8 (4): 124–28.
- Saetersdal, Magne, John M. Line, and H. J. B. Birks. 1993. "How to Maximize Biological Diversity in Nature Reserves Selections: Vascular Plants and Breeding Birds in Deciduous Woodlands in Western Norway." *Biological Conservation* 66 (2): 131–38.
- Solow, Andrew, Stephen Polasky, and James Broadus. 1993. "On the Measurement of Biological Diversity." *Journal of Environmental Economics and Management* 24 (1): 60–68.
- Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. "What to Protect?—Systematics and the Agony of Choice." *Biological Conservation* 55 (3): 235–54.
- Weitzman, Martin. 1992. "On Diversity." Quarterly Journal of Economics 107 (2): 363–406.

- Williams, Paul H., and Chris J. Humphries. 1996. "Comparing Character Diversity Among Biotas." In *Biodiversity: A Biology of Numbers and Difference*, ed. K. J. Gaston. Oxford: Clarendon Press.
- Williams, Paul, David Gibbons, Chris Margules, Anthony Rebelo, Chris Humphries, and Robert Pressey. 1996. "A Comparison of Richness Hotspots, Rarity Hotspots and Complementary Areas for Conserving Diversity Using British Birds." Conservation Biology 10 (1): 155–74.
- Willis, Christopher K., Amanda T. Lombard, Richard M. Cowling, Barry J. Heydenrych, and Chris J. Burgers. 1996. "Reserve Systems for Limestone Endemic Flora of the Cape Lowland Fynbos: Iterative Versus Linear Programming Techniques." *Biological Conservation* 77 (1): 53–62.
- Wilson, E. O. 1988. "The Current State of Biological Diversity." In *Biodiversity*, ed. E. O. Wilson and E. Peter. Washington, D.C.: National Academy Press.